

**RECONSIDERATION OF THE STATUS OF THE GENERA  
PHYLLOMACROMIA AND MACROMIA  
(ANISOPTERA: CORDULIIDAE)**

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Although the genus *Phyllomacromia* Selys, 1878 has for over 40 years generally been considered synonymous with *Macromia*, a recent study of the male secondary genitalia and caudal appendages has shown these genera to be distinct. They differ markedly in the morphology of the penis, genital ligula, and epiproct, and typically also in that of the cerci and posterior hamules. The forms of the penis and genital ligula of *Phyllomacromia* are more similar to those of *Epophthalmia* than to *Macromia*, while *Macromia* most closely resembles *Didymops* in these characteristics. *Phyllomacromia* probably includes all the African species recently attributed to *Macromia*.

**INTRODUCTION**

According to the most recent catalog of Odonata (BRIDGES, 1994), the genus *Macromia* comprises 117 species and is virtually cosmopolitan, being absent only from the Neotropics and northern Europe. It has apparently undergone major radiations in Africa and in southern Asia and a smaller one in northeastern Asia and North America. The species are mostly quite similar in general appearance, although they vary in size, extent of yellow maculation, genitalic structure, and, in a few cases, details of venation and wing shape. Several "species groups" have been recognized on these bases (e.g., GAMBLES, 1979; LAIDLAW, 1922; LIEFTINCK, 1929, 1971), but little progress has been made at elucidating relationships within the genus as a whole or at clarifying their relationships with other macromiines.

SELYS (1878) erected the genus *Phyllomacromia* for *Macromia africana* Selys, *M. trifasciata* Selys, and *M. tropicalis* Selys; KIRBY (1890) later designated *M. trifasciata* as the type. These were distinguished primarily on the bases of possess-

ing, supposedly, only a single row of cells in the discoidal field of the forewings and lacking a dorsal spine on abdominal segment 10 (other characters listed are shared with many other *Macromia*). RIS (1921), among others, found these characters unreliable, however, and did not recognize *Phyllomacromia*, although the name continued in common use until 1954. At that time FRASER (1954), based on examination of a large series of specimens that included nearly all the African species then known, convincingly argued that the two critical characters are not congruent in their distribution among species and that the number of discoidal field cell rows is highly variable even within species. Moreover, he synonymized *M. tropicalis*, one of the original *Phyllomacromia* species, with *Macromia picta*; subsequently *M. africana* has also been considered a synonym of *M. picta* (BRIDGES, 1994), leaving only *M. trifasciata* as a good species. *Phyllomacromia* has hardly been used since Fraser's paper.

Ironically, in view of the evidence to be presented here, PINHEY (1951) reported that "Fraser tells me (Aug., 1948) that he now considers all the African species should be relegated to *Phyllomacromia*, on genitalial grounds, particularly characters of the penis." I do not know why Fraser reversed his position in subsequent years, unless it was because of the lack of generic characters distinguishing females, but I believe his 1948 opinion was entirely correct, and the object of this paper is to support that assertion.

At the 13th International Symposium of Odonatology, in Essen, Germany, Peter Miller and I first discussed some of the curious variations in penile morphology found in macromiines. In the following few months we developed preliminary plans to investigate this further, I from the standpoint of systematics, he from that of functional morphology. His untimely death prevented our collaboration. It is with a considerable sense of personal loss that I dedicate this paper to his memory, in the hope that it will augment our understanding of African dragonflies, to whose study Peter made so many contributions.

#### MATERIAL AND METHODS

Visual observations and drawings were made with a Wild™ stereomicroscope equipped with a camera lucida. When possible, structural details of the penes and accessory secondary genitalia were examined using an Hitachi™ S510 electron microscope after coating with gold-palladium. Descriptive terminology for the male caudal appendages is that of SNODGRASS (1954) and for the secondary genitalia that of PFAU (1971), except that in the latter case I use "genital ligula" in place of "ligula" to distinguish this structure from the labial ligula.

Collections from which material was obtained are designated using the following acronyms: AB - Collection of ALLEN BARLOW; ANSP - Academy of Natural Sciences of Philadelphia; FSCA - Florida State Collection of Arthropods; MLM - Collection of M. L. May; NMNH - National Museum of Natural History (Smithsonian Institution; Washington); TWD - Collection of T. W. DONNELLY.

## RESULTS

Species examined are listed in Table I and are scored with respect to characters of the penis, ligula, posterior hamules, cerci, epiproct and shape of the abdomen. The differences between African species (hereafter, *Phyllomacromia*) and all others are striking, especially in the morphology of the penis. All of the former have extremely narrow distal penile segments ending in a relatively short distal median process of the fourth segment and three long, slender flagella, as shown for *picta* in Figure 1 (the distal segments and base of the flagella the penis of *trifasciata* appear in Fig. 3D; flagella mostly concealed). True *Macromia* have stouter distal segments, with the median process longer and with only one or two flagella and a much shorter, flap-like basal lobe that may be homologous with the third flagellum of African forms, as in *M. illinoensis georgina* (Fig. 2A, B) and the type species of the genus, *M. cingulata* (Fig. 5D). Very little variation is evident within the African group; somewhat more occurs within *Macromia* proper, but in all these the general structure is as in the two species illustrated. The genital ligula of *Phyllomacromia* is narrow and cupped at the end (Fig. 1D), while that of *Macromia* is wide and

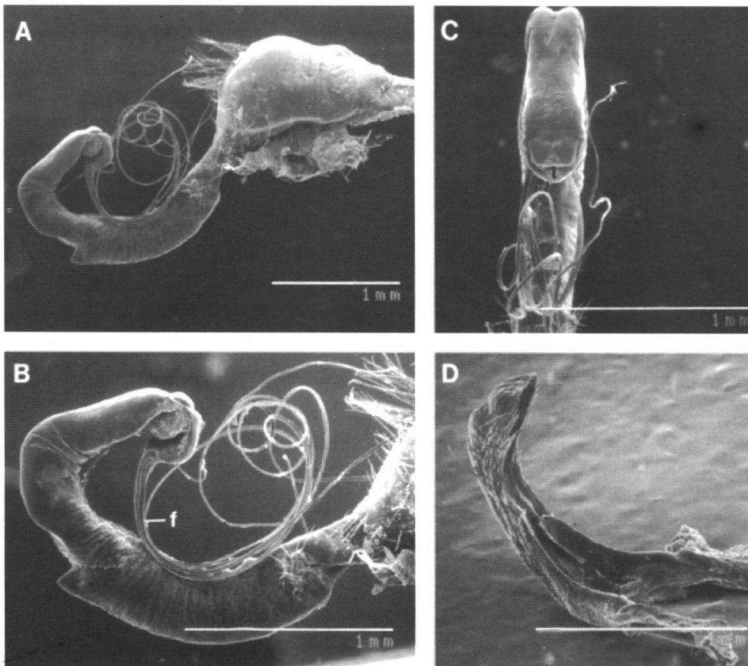


Fig. 1. *Phyllomacromia picta* (Malawi, Mt. Mulamje, 22-XI-1992, leg. Murphy, AB): - (A) whole penis, lateral view; - (B) distal segments of penis, lateral view, f - flagella; - (C) distal segments of penis, posteroventral view; - (D) isolated genital ligula, posterolateral view. - [Scale bars = 1.0 mm]

Table 1

Species of macromiines examined, with states of selected characters indicated; see text for description of character states. "Abdominal expansion" is the ratio of the maximum width in lateral view of the eighth segment to the minimum width of the fifth. In some cases, indicated by "?", I could not determine with complete reliability whether one or two penis flagella were present because of breakage or because I could not extrude the penis completely, but it is certain that none of these had three flagella. — [Asterisks indicate type species of the genera]

Genus	Species	Penis stature	Penis med. process	No. of penis flagella	Genital ligula	Posterior hamule	Cercus lat. tooth	Epipect tip	Abdomen expansion	Abd. with spine
<i>Macromia</i>	<i>allegghianensis</i>	robust	well-dev.	1	flat	tapered	reduced	narrow	1.6	no
	<i>amphigena</i>	robust	well-dev.	1	flat	tapered	yes	narrow	1.7	no
	<i>cincta</i>	robust	well-dev.	2?	flat	tapered	yes	narrow	≤2	yes
	* <i>cingulata</i>	robust	well-dev.	2	flat	intermediate	yes	narrow	2.0	yes
	<i>illinoensis</i>	robust	well-dev.	1	flat	tapered	variable	narrow	1.7	no
	<i>magnifica</i>	robust	well-dev.	1	flat	tapered	no	narrow	1.7	no
	<i>melpomene</i>	robust	well-dev.	1	flat	tapered	yes	narrow	2.1	yes
	<i>moorei</i>	robust	well-dev.	2?	flat	tapered	yes	narrow	≤2	no
	<i>pacifica</i>	robust	well-dev.	1	flat	tapered	yes	narrow	1.6	no
	<i>splendens</i>	robust	well-dev.	1?	flat	tapered	yes	narrow	1.6	no
	<i>taeniolata</i>	robust	well-dev.	1	flat	tapered	yes	narrow	1.5	no
	<i>terpsichore</i>	robust	well-dev.	1	flat	tapered	reduced	narrow	2.1	no
	<i>tillyardi</i>	robust	well-dev.	1	flat	tapered	yes	narrow	≤2	yes
	<i>westwoodi</i>	robust	well-dev.	2?	flat	tapered	yes	narrow	≤2	yes
	<i>zeylanica</i>	robust	well-dev.	2	±flat	intermediate	yes	narrow	1.9	reduced
<i>Phyllocromia</i>	<i>aeneothorax</i>	slender	vestigial	3	cupped	abrupt hook	no	broad	2.5	yes
	<i>bifasciata</i>	slender	vestigial	3	cupped	abrupt hook	no	broad	3.1	no
	<i>funicularia</i>	slender	vestigial	3	cupped	abrupt hook	no	broad	2.9	yes
	<i>monoceros</i>	slender	vestigial	3	cupped	abrupt hook	no	broad	2.6	yes
	<i>nyanzana</i>	slender	vestigial	3	cupped	abrupt hook	no	broad	3.0	no
	<i>picta</i>	slender	vestigial	3	cupped	abrupt hook	no	broad	3.2	yes
	* <i>trifasciata</i>	slender	vestigial	3	cupped	abrupt hook	no	broad	3.1	no
<i>Didymops</i>										
	* <i>iransversa</i>	robust	well-dev.	1	flat	tapered	no	narrow	1.9	no
<i>Epophthalmia</i>	<i>elegans</i>	intermed.	vestigial	3	cupped	abrupt hook	yes	narrow	2.3	yes
	* <i>vittata</i>	intermed.	vestigial	3	—	abrupt hook	no	narrow	—	no

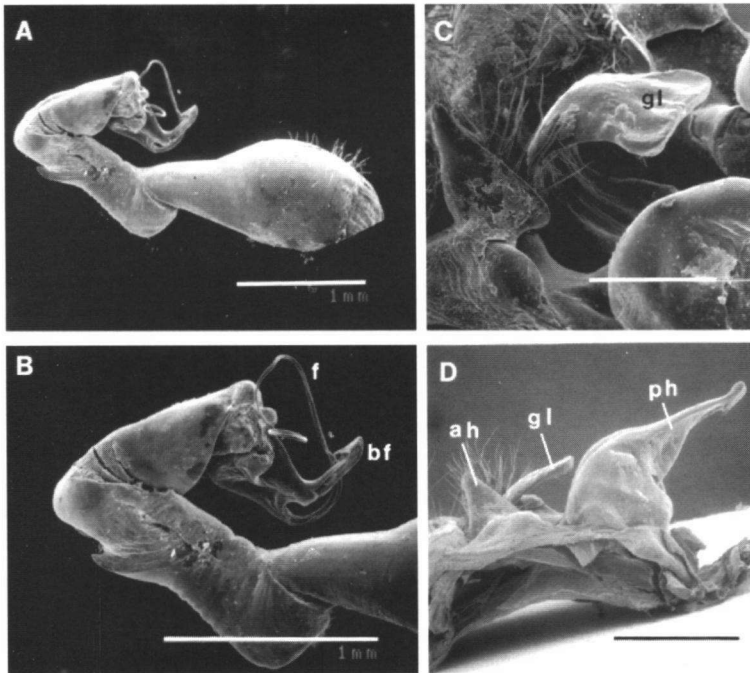


Fig. 2. *Macromia illinoiensis georgina* (U.S.A., FL, Gadsen Co., 13-IX-1972, coll. May, MLM): - (A) whole penis, lateral view; - (B) distal segments of penis, lateral view, bf - basal flap, f - flagellum; - (C) genital ligula (gl) in situ, oblique posterolateral view; - (D) accessory secondary genitalia, lateral view, ah - anterior hamule, ph - posterior hamule. - [Scale bars = 1.0 mm in A, B, D; 0.5 mm in C]

curled along its longitudinal axis but with very little side-to-side curvature (Fig. 2C, D).

In addition to the differences in penile morphology, the cerci and epiproct differ. The cerci of African species all lack a lateral tooth and generally have little sign of a laterobasal carina (*trifasciata*, Fig. 3, exhibits maximum development of this feature) but do have irregularly spaced ventral denticles extending nearly to their base. All *Macromia* have a distinct lateral tooth, except for a few North American species in which only a strong laterobasal ridge is present, and ventral denticles are practically confined to the portion distal to the lateral tooth or the end of the ridge. The epiproct of *Macromia* tapers to a narrow point, so that the terminal denticles are separated by less than the width of one of them (Fig. 5B), while in *Phyllomacromia* the distal end is broad, the denticles separated by distinctly more than the width of one (Fig. 3C). Differences in the hamules and expansion of the terminal abdominal segments are also recognizable, although less consistent than the preceding characters. In African macromiines the posterior hamules are quite stout for most of their length, generally abruptly contracting to a fine hook only in

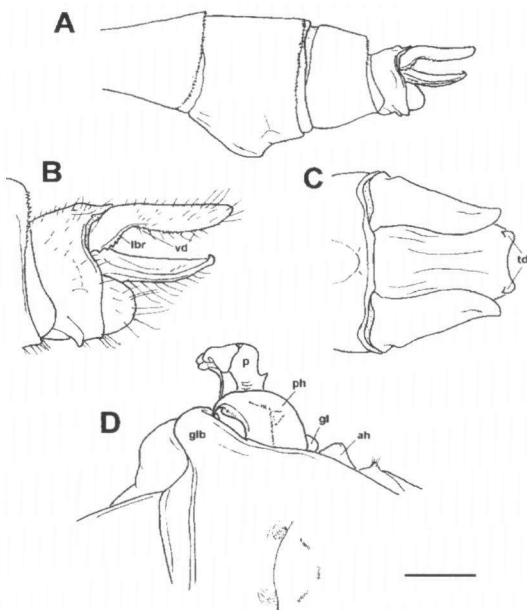


Fig. 3. Male reproductive structures of *Phyllomacromia trifasciata* (Madagascar, Prov. Fianarantsoa, nr Ranomafana, 4-III-1990, coll. E. Steiner, TWD): - (A) terminal abdominal segments, lateral view; - (B) caudal appendages and tenth abdominal segment, lateral view, lbr - laterobasal ridge, vd - ventral denticles; - (C) caudal appendages, dorsal and slightly posterior view, td - terminal denticles of epiproct; - (D) secondary genitalia (inverted), lateral view, ah - anterior hamule, gl - genital ligula, glb - genital lobe, p - penis, ph - posterior hamule. - [Scale bar = 2.0 mm in A; 1.0 mm in B-D]

abdominal segment. When present, however, that of *Phyllomacromia* is unusual in that the upper end of the solid portion of the spine is rounded and generally not much laterally compressed but is tipped with a very dense, tapering brush of stout setae that often appears to be a solid extension of the spine (Fig. 4A); some species (e.g., *bifasciata*) may retain the setal brush even when the solid spine is nearly obsolete. *Macromia* never have such a setal brush (Fig. 5A) and the spine usually is strongly laterally compressed.

## DISCUSSION

Apomorphies (compared to likely sister taxa of the macromiines, such as *Macromidia* [LIEFTINCK, 1971] or *Idomacromia*, or the *Oxygastra-Neocordulia-Micromidia* group of genera [FRASER, 1957; MAY, 1995, and unpublished observa-

about the distal 1/5 or less of their visible length (Figs 3D, 4B), whereas those of *Macromia* usually taper more smoothly for at least 1/3 to 1/2 of their length, and often more (Fig. 2D; somewhat more abruptly narrowed in *M. cingulata*, Fig. 5C, and even more so in *zeylanica* and probably in *ellisoni* [FRASER, 1936]). Finally, the terminal abdominal segments are more widely expanded in most *Phyllomacromia* (Fig. 3A), in lateral view at least 2.5 times as broad at the widest point of segment 8 as the slender middle segments (an exception, based on illustrations in the original description, may be *P. caneri*; GAUTHIER, 1987); in *Macromia* the same ratio is no more than 2.1:1 (Tab. I).

Both *Macromia* and *Phyllomacromia* may or may not have a strong, dorsal, spine-like process on the tenth ab-

tions]) uniting *Phyllomacromia* are principally the morphology of the penis and also the broad tip of the epiproct, broad and unbranched posterior hamuli, and very widely expanded 8th and 9th abdominal segments. *Macromia*, on the other hand, is characterized by the curled but not scooplike genital ligula (shared with most higher corduliids; very slightly scooplike in *M. zeylanica*), unbranched and narrowly tapering posterior hamuli (with possible exceptions noted above), and hypertrophy of the lateral cercal teeth (which I interpret as secondarily lost in some North American species).

All these distinctions rest on characters of the males only, and I have not discovered features that are useful in discriminating females of *Phyllomacromia* from *Macromia*, although the internal genitalia almost certainly differ, and structures of the head where the male cerci and epiproct grip may do so; larval characters have not been investigated owing to lack of material. Some workers on Odonata have considered differences in one sex only as insufficient to justify recognition of generic differences, although, aside from the practical difficulty in identification, there is no theoretical reason not to do so. In this instance, moreover, there are good reasons to do so if taxonomic stability of macromiines is to be maintained. For at least the past 60 years, the genera *Didymops* and *Epophthalmia* have been almost universally regarded as distinct. Some evidence suggests, however, that *Didymops* may be more closely related to *Macromia* and *Epophthalmia* to *Phyllomacromia* than are *Macromia* and *Phyllomacromia* to each other. In particular, the penis structure of *Didymops* (Fig. 6A) is very similar to that of most *Macromia*, its genital ligula is curled and not scoop-shaped, and its posterior hamules taper for most of their length. *Epophthalmia*, by contrast, have penes remarkably like *Phyllomacromia* although not so slender and elongate (Fig. 6B), a scooplike genital ligula, and broad posterior hamules that are abruptly narrowed distally (albeit with a bifid tip that is absent in *Phyllomacromia*). The resemblance in penis structure between *Epophthalmia* and *Phyllomacromia* is particularly telling because it is complex, involving resemblances in a number of distinct features, and it is unique within the corduliines and thus almost certainly a synapomorphy of these two genera. While sister-group relationships among the macromiine genera have yet to be worked out in detail, the likelihood is very high that any arrangement recognizing *Didymops* and *Epophthalmia* but not *Phyllomacromia* would be

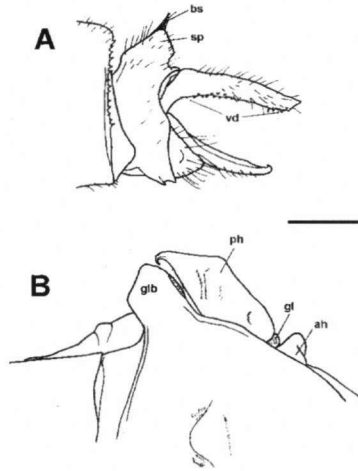


Fig. 4. Male reproductive structures of *Phyllomacromia picta* (data as in Fig. 1): - (A) caudal appendages and tenth abdominal segment, lateral view, bs - brush of stiff setae, sp - spine of 10th abdominal segment, vd - ventral denticles; - (B) secondary genitalia (inverted), lateral view, symbols as in Fig. 3D. - [Scale bar = 1.0 mm]

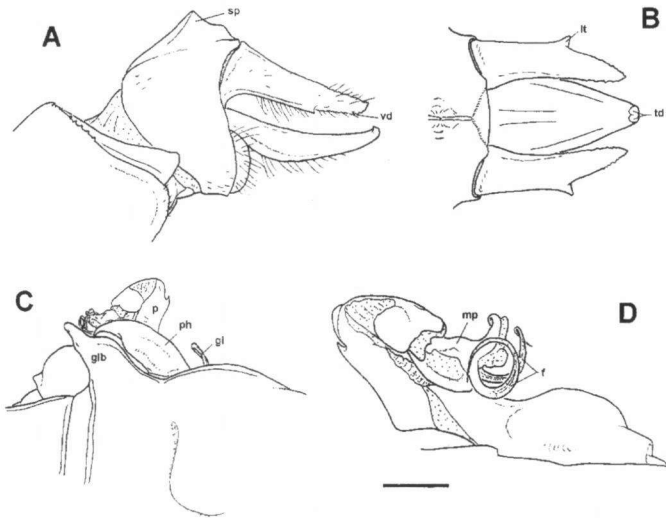


Fig. 5. Male reproductive structures of *Macromia cingulata* (India, Mahabaleshwar, 22-IV-1922, leg. Fraser, ANSP): - (A) caudal appendages and tenth abdominal segment, lateral view, sp - spine of 10th abdominal segment, vd - ventral denticles; - (B) caudal appendages, dorsal view, lt - lateral tooth of cercus, td - terminal denticles of epiproct; - (C) secondary genitalia (inverted), lateral view, symbols as in Fig. 3D; - (D) penis, lateral view, fl - flagella, mp - median distal process. - [Scale bar = 1.0 mm in A-C; 0.5 mm in D]

paraphyletic.

I should note at this point that the monophyly of the macromiines as a group is well supported by the following synapomorphies: sectors of the arculus fused for more than 1/2 the length of the arculus (shared with *Idionyx* and *Macromidia*); hindwing triangle far distad from the arculus and elongate in the axis of the wing; anal loop compact, without a midrib; ventral tooth of the tarsal claws enlarged (shared with *Macromidia*); anterior hamules large and erect; posterior hamules not branched and more or less laterally compressed (shared with the higher cordulines). Several of these characters, especially of the hindwing triangle, anal loop, and anterior hamules, have often been regarded as plesiomorphies, but I have extensive evidence (May, unpublished data) that they are not.

In summary, I believe the evidence is very strong that *Phyllomacromia* should be resurrected and probably should include all the African species hitherto placed in *Macromia*. Although I have only examined specimens of 7 of the 40 species involved, illustrations of the penes of *aequatorialis* and *hervei* (LEGRAND, 1980), *aureozona* (PINHEY, 1966), *bicristulata* (LEGRAND, 1975) and *villiersi* (LEGRAND, 1992) show that the morphology of these is very close to that of *picta*, while illustrations of the cerci, epiproct, and posterior hamules of numerous other species agree with the characterizations I have given above (e.g., FRASER, 1954; GAMBLES, 1971, 1979; GAUTHIER, 1987; LINDLEY, 1980), and no il-



illustrations or descriptions contradict any of them.

*Macromia* is more widespread and diverse, and I have found very few instances in which the penes were illustrated. Nevertheless, I have been able to examine representatives of most major groups (Tab. I), and the extensive, accurate and detailed illustrations of ASAHINA (1964, 1983, 1987), FRASER (1936), and especially LIEFTINCK (e.g., 1929, 1950, 1952, 1955, 1971) provide a broad sample of other relevant characters. It may eventually prove desirable to split *Macromia* further, based, e.g., on such characters as differences in numbers of penile flagella and/or hamule shape (Tab. I, and cf. Figs 1 and 2 vs. Fig. 5), but that effort will require close examination of many species, including more attention to female and larval characteristics.

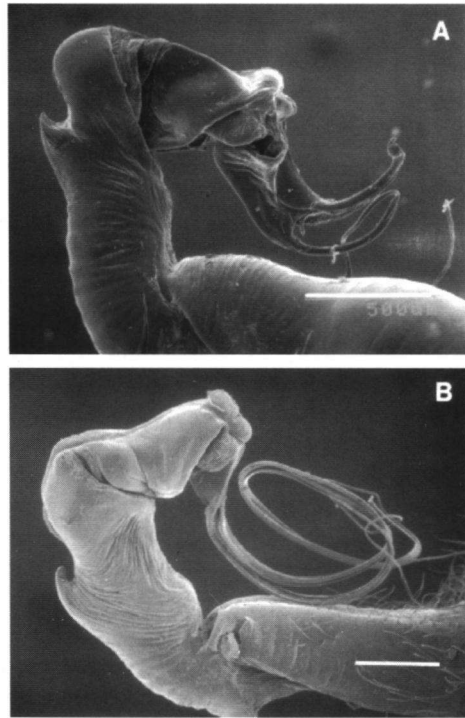


Fig. 6. Distal segments of penes of: (A) *Didymops transversa* (U.S.A., FL, Santa Rosa Co., 5-IV-1975, coll. May, MLM); - (B) *Epophthalmia elegans* (B; China, Szechwan, Suifu, IX/X-1922, coll. Graham, NMNH). - [Scale bars = 0.5 mm]

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